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Geographic variation in *Poecilia* Bloch and Schneider, 1801 (Teleostei: Poeciliidae), with descriptions of three new species and designation of lectotypes for *P. dovii* Günther, 1866 and for *P. vandepolli* van Lidth de Jeude, 1887

Fred. N. Poeser

Zoological Museum of Amsterdam, Department of Ichthyology, P.O. Box 94766, 1090 GT Amsterdam, The Netherlands

Abstract.—The South American cyprinodontiform fish species with the vernacular name "mollies" are analyzed and three new species of the genus *Poecilia* are described and figured, viz., *P. boesemani,* n. sp. from Port of Spain, Trinidad, *P. koperi,* n. sp. from coastal areas of Venezuela and Colombia, and *P. wandae,* n. sp. from the Zulia district, Venezuela, west of Lake Maracaibo. Thirteen species of *Poecilia* are presently recognized from the northeastern part of South America and adjacent islands, viz., six mollies (including *P. vivipara* and *P. caucana*), five micropoeciliids, *P. heterandria* and the guppy (*P. reticulata*). Two different populations in both *P. koperi* and *P. wandae* are recognized, based on variation in pigmentation. From the type series of *P. dovii* Günther, 1866 and *P. vandepolli* Van Lidth de Jeude, 1887 lectotypes are selected. Four subspecies of *P. gillii* are recognized as morphologically and geographically distinct populations.

Poecilia reticulata, P. heterandria, P. bifurca, P. parae, P. picta, P. branneri and *P. minima* are not considered herein, whereas *P. laurae* remains a species inquirendae. A geocline in characters of the species of *Poecilia* is recorded and an evolutionary scenario is discussed.

This paper seeks to extend our biogeographic knowledge of the genus *Poecilia* Bloch & Schneider, 1801 and describes three new species from the southern end of the range of this genus. The present study records seven species from the northeastern part of South America. Whereas the number of poeciliid species constitutes a dominant part of the Central American fish fauna, this is not the case in South America. Miller (1983) constructed a key and checklist for the Mexican species, but there are no comprehensive lists for the species of *Poecilia* from Central and South America. Specimens of the species herein described as new, viz., *P. koperi, P. boesemani* and *P. wandae,* were previously identified as either *P. vivipara* Bloch & Schneider, 1801; *P. sphenops* Valenciennes, 1846 (Regan 1913: 1013; Price 1955:18; Boeseman 1960:122); *P. vandepolli* van Lidth de Jeude, 1887 (de Beaufort 1940:111; Schultz 1949:84, 97–99; Feltkamp and Kristensen 1969); or mentioned as 'unidentified species' (Rosen & Bailey 1963:48).

Regan (1906–08) examined variation within the species of *Poecilia* and extended our knowledge of the expression of morphology and pigmentation (Regan 1906–08, fig. 13), as well as the geographic range (from northern Mexico to the Leeward Islands) of the *P. sphenops* complex.

With the discovery of the structures of the gonopodial tip as a taxonomic tool (Eigenmann 1907), Regan (1913) reorganized species groups in the subfamily Poeciliinae.

With respect to the *P. sphenops* complex, he allocated *P. sphenops* to the genus *Mollienesia* on the basis of identical gonopodia of *M. latipinna* and *M. sphenops.* Moreover, the number of dorsal fin rays of *M. formosa* was intermediate between the numbers found in *M. latipinna* and *M. sphenops,* which therefore rendered the character invalid. Although Regan did not mention *P. vandepolli,* the geographic range of his *M. sphenops* still included the Leeward Islands, i.e., the Lesser Antilles.

The importance of the gonopodial tip was also recognized by Hubbs (1924), who used the gonopodium as "the chief distinctive feature of the Poeciliidae (as here delimited)." The *M. sphenops* group was defined by Hubbs (1926) as "the multitude of races allied to, or inseparable from *M. sphenops.*" This group was separated from *M. latipinna* and allies by the number of dorsal fin rays. For *M. sphenops,* Hubbs was "unable to delimit, in either distribution or in characters, any multitude of elementary species making up the *sphenops* complex of Middle America. The problem of determining the relationships of the diverse types, many of which have received specific names, is in prospect a most fascinating study."

The situation remained promising, even after the revision of Rosen and Bailey (1963), who listed a total of 35 nominal species in their synonymy of *P. sphenops.* Schultz and Miller (1971) mentioned: ". . . a thorough study of the whole complex and the type specimens will be required before systematic units and the nomenclature can be convincingly coordinated." Species recognition was aided by dental analyses (Schultz and Miller 1971), i.e., unicuspid and tricuspid species were recognized. Other alpha-taxonomic features (meristic and morphologic characters, body and fin color, even allozyme data) remained confusing. Rivas (1978) remarked that "proportional body measurements are [to be] omitted . . . , there is considerable variation in characters individually, ontogenetically, seasonally, geographically, and environmentally and, therefore, they are of little or no value in distinguishing species (except in relative fin position)." Extensive and detailed investigations (Schultz and Miller 1971, Menzel and Darnell 1973, Miller 1975) resulted in a checklist for the Central American mollies (Miller 1983), which included eight species of Central American short-finned mollies. No species were mentioned from outside this range. Comparisons of the Mexican species to those of Central and South America (Poeser 1992, 1995, 1998) have led to the present study.

Methods

Some 17 lots of *Poecilia vandepolli,* including the type series of *P. vandepolli vandepolli* and *P. v. arubensis,* have been reexamined. From the type series, a lectotype is selected. Meristic data and inner jaw dentition (cf. Schultz and Miller 1971) received special attention. Vernier calipers were used to record distances to 0.1 mm. The average of the measurements and counts are given and compared to a similar study of Feltkamp and Kristensen (1969) and to the data of *P. vivipara* and of *P. gillii.*

In the description of the new species, proportional morphometric values (Table 2) are recorded in thousandths of the standard length (SL), following Miller (1975). The small size of *P. wandae* made measurements difficult to impossible and therefore some were omitted. Meristic characters follow Hubbs and Lagler (1947). In the type series of *P. wandae,* all specimens have damaged caudal fins; therefore, the caudal fin ray count is estimated. Terms concerning the shape of inner jaw dentition follow Garman (1895). Melanophore pigmentation of preserved specimens and gonopodial structures are also recorded (Figs. 1 to 4).

The combined data are used to evaluate relationships between the newly described species. A key to the species is provided in Appendix 1.

The following abbreviations are used in the species diagnosis provided below.

A = anal fin rays
BS = scales around the body
CPD = least depth of the caudal peduncle
CPS = scales around the caudal peduncle
D = number of dorsal fin rays
G = gonopodial ray
LLS = lateral scales
P = pelvic fin rays
PL = predorsal length
PS = predorsal scales
SL = standard length

Systematics

The genus *Poecilia* is diagnosed by the shape of gonopodial ray 4p, which has six to fourteen unserrated distal segments, followed by dorsally serrated subdistal segments (cf. Miller 1975). The genus consists of several ill-defined subgenera. A more detailed analysis is in progress.

In the subgenus *Poecilia,* ventral spine-like serrae are present on the third gonopodial ray. Gonopodial rays 4a and 4p are very similar, as are rays 5a and 5p. The *P. sphenops* species group has terminal segments of gonopodial ray 4a and of gonopodial ray 4p close to each other, giving the gonopodium a sharp appearance. The members of this species group are moderately sized to large, with nuptial specimens usually larger than 35 mm SL. The members of the *P. caucana* species group are defined by the relative thickness of gonopodial ray 4p versus 4a. The tips of these rays are split, making the gonopodium blunt. Nuptial specimens are less than 35 mm SL.

Poecilia vivipara Bloch & Schneider, 1801

Poecilia vivipara Bloch & Schneider, 1801: 452, pl. 86, Fig. 2 (type locality: Surinam).

Poecilia surinamensis Humboldt & Valenciennes, 1821:158 (type locality: Surinam, French Guyana, Brazil).

Poecilia unimaculata Humboldt & Valenciennes, 1821:158 (type locality: Brazil, Rio de Janeiro).

Poecilia schneideri Humboldt & Valenciennes, 1821:159 (type locality: Surinam).

Neopoecilia holacanthus Hubbs, 1924:11 (type locality: Puerto Rico, introduced).

Material.—West Indian Antilles: ZMA 120.384 (22), St. Lucia, freshwater pool, ±1 km west from Fort Vieux, coll. J. H. Stock, 20-II-1974.

Guyana: BMNH 1974. 10. 10. 527–619 (7 out 93), Georgetown, Seawall trench, no date; CAS 59364 (12), Georgetown trenches, C. H. Eigenmann 1908; CAS (SU) 21784 (2), same data as CAS 59364; USNM 66278 (2), same data as CAS 59364; ZMA 100.629 (2), same data as CAS 59364; ZMA 119.912 (3), East Coast Demerara, Turkeyen, drainage canal, coll. M. Tamessar, 28-I-1987; ZMA 119.913 (6), East Coast Demerara, Bel Air, stagnant ditch, coll. M. Tamessar, 28-I-1987; ZMA 119.917 (4), East Coast Demerara, Industry, shallow pool, coll. M. Tamessar, 28-I-1987; ZMA 121.005 (5), Guyana, coll. F. Vermeulen, no date; ZMA 121.007 (15), Guyana, coll. F. Vermeulen, 1992; ZMA 121.009 (5), Guyana, coll. F. Vermeulen, 1992.

Surinam: MNHN B. 932 (5 syntypes of *P. surinamensis*), Surinam River, Levaillant, no date; MNHN 4391 (48 syntypes of *P. surinamensis*), Cayenne, Rousseau, no date; MNHN B. 918 (60), without exact locality, Duvernoy, no date; RMNH 18516 (2), Surinam, coll. J. Th. Noordijk, August 1887; ZMA 105.332 (2), Paramaribo-west, garden canals, coll. H. Nijssen, 12-XII-1966; ZMA 106.757 (16), Marowijne River, coastal plain on Tijgerbank, west of mouth, coll. H. Nijssen, 1-IV-1966; ZMA 115.118 (45), Surinam district, Lagoon 7 & 8, 05°59′N, 54°49′W, coll. M. P. Panday, 22-IV-1974; ZMA 115.121 (20), same data as ZMA 115.118; ZMA 119.908 (6), Surinam River, pool near beach at Braamspunt, coll. I. Kristensen, 14-III-1960; ZMA 121.000 (4), Paramaribo, Mason Street, pol-

luted trench, coll. F. Vermeulen & W. Suyker, 24-III-1991.

French Guiana: USNM 121833 (9), Cayenne, Carriera Guila, S. F. Yolles 1945; USNM 121834 (2), Cayenne, Pont Magie, S. F. Yolles 1945; USNM 121835 (9), Cayenne, Ruisseau de l'institute-eau douce, S. F. Yolles 1945; USNM 149938 (4), Cayenne, S. F. Hildebrand 1945.

Brazil: RMNH 2724 (2 syntypes of *P. unimaculata*), Rio de Janeiro, coll. Delalande, no date; ZMA 100.628 (1), Brazil, coll. Moesch, 1884; ZMA 116.210 (14), Rio Grande do Norte, Rio Açu (Rio Assu), downstream of Macau, coll. R. Boddeke, 10-I-1979.

Diagnosis.—A = 8; D = 7; C = 16–18; LLS = 24–26; CPS = 16. *Poecilia vivipara* may have a midlateral spot or blotch in both sexes, a unique character in the subgenus. The gonopodium has no extruding hooks or spines, gonopodial ray 4a with serrae on dorsal surface.

Description.—Medium sized species, mature males smaller than 50 mm and females smaller than 60 mm. The body is truncate and displays dark stripes on the sides. The caudal and dorsal fins have black markings, with broad yellow margins. The caudal fin has black margins, at the base broader than at the terminal end. There is some variation in the presence or absence of the spot at the side of the body. No extensive records are available of the extent of this variation. In the populations in which it is present, the blotch is also prominent in young specimens. The gonopodium is figured in Miller (1975), the presence of dorsal serrae on ray 4a are unique within the subgenus.

Distribution.—*Poecilia vivipara* is found in coastal habitats from Venezuela to Argentina. It is also found on some islands of the Lesser Antilles.

Remarks.—Garman (1895) diagnosed this species and provided a list of synonyms. He also explained the obvious aberrant figure in the original description. Hubbs (1926) synonymized *Neopoecilia holocanthus,* correcting his misidentification.

Poecilia mexicana Steindachner, 1863

Poecilia mexicana Steindachner, 1863:178, pl. 4, fig. 1, 1a (type locality: Mexico, Orizaba).

Poecilia thermalis Steindachner, 1863:181, plate 4, fig. 3, 3a (type locality: Central America, warm springs).

?*Gambusia* (?) *modesta* Troschel, 1865:105 (type locality: Mexico).

?*Gambusia* (?) *plumbea* Troschel, 1865:106 (type locality: Mexico).

Poecilia chisoyensis Günther, 1866:342 (type locality: River Chisoy, Vera Paz).

Poecilia dovii Günther, 1866:344 (in part; type locality: Mexico; lectotype is *P. gillii*).

Poecilia limantouri Jordan & Snyder, 1900: 116–117, 129–131 (type locality: Tampica, Tamaulipas, Mexico).

Mollienesia sphenops vantynei Hubbs, 1935:11, plate 2, fig. 1 (type locality: Guatemala, Uaxactum, Rio Hondo).

Mollienesia sphenops macrura Hubbs, 1935:12, plate 2, figs. 2–3 (type locality: Guatemala, Rio San Pedro de Martir).

Mollienesia sphenops altissima Hubbs, 1936:239, plate 9, figs. 1–3 (type locality: Mexico, Yucatan Peninsula, Miramar Spring).

Mollienesia sphenops melanistia Hubbs, 1937 (type locality: Mexico, Tamaulipas, Arroyo Marmoleyo).

Material.—Barbados: BMNH 1970.1.29: 1 (1) Barbados, coll. R. Heath, no date; RMNH 24814 (55), rivulet near Three Mills (13°10′N, 59°27′W), coll. I. Kristensen, 13.6.1961; RMNH 24804 (6), rivulet at Three Mills (13°10′N, 59°27′W), coll. I. Kristensen, 13.6.1961; RMNH 24809 (5), rivulet near Three Mills (13°10′N, 59°27′W), coll. I. Kristensen, 13.6.1961.

Diagnosis.—A = 9; D = 9–10; C = 18–22; LLS = 26–27; CPS = 18.

Description.—*Poecilia mexicana* is rather variable in its morphology. This is a trun-

cate, torpedo shaped species in northern Mexico but ranges to high, laterally flattened specimens at the eastern end of the range in the Yucatan Peninsula. While the northern populations possess deeply blue pigmented bodies, alpha-males of the Yucatan populations have a more copper-red body. The fin pigmentation is also varying, from totally black at the base of the fin with an orange outer area (in northern populations) to a black and yellow reticulate pattern (on the Yucatan Peninsula). Between these extremes clinal variation is noted.

In the Barbados material, both males and females exhibit considerable variation in their pigmentation, especially the specimens in RMNH 24804 have many spots on their body (perhaps a basis for why they were separated from the other lots). Females have nine anal fin rays, some females have 10 dorsal fin rays. The membranous hook on gonopodial ray 3 is extremely small, without a bony spine. Several specimens have 20 caudal fin rays, whereas all specimens have 18 scales around the caudal peduncle.

The diagnostic features of *P. mexicana* generally most closely agree with the nominal subspecies *P. gillii gillii* (see below), with the exception of the number of scales around the caudal peduncle (18 versus 16 in *P. gillii*).

Distribution.—*Poecilia mexicana* occurs on the Atlantic coast of Central America, from the Texas border, through Yucatan into Guatemala and Costa Rica. The population found on Barbados is probably derived from escaped aquarium specimens, which is confirmed by their abnormal variability in body pigmentation.

Poecilia gillii
(Kner & Steindachner, 1864)

Xiphophorus Gillii Kner and Steindachner, 1864: in Kner & Steindachner, 1865:25 (type locality: Panama, Rio Chagres); *Poecilia gillii*; Günther, 1868:395; *Poecilia sphenops gillii*; Hubbs, 1953:145.

Poecilia mexicana [non Valenciennes, 1863]; Poeser, 1992:86 (misidentification).

Poecilia thermalis [non Steindachner, 1863] Günther, 1866:341 (type locality: San Salvador, warm springs).

Poecilia dovii Günther, 1866:344 (in part: type locality: Lake of Nicaragua).

Platypoecilus mentalis Gill, 1876:335 (type locality: Isthmus of Panama).

Poecilia Boucardi Steindachner, 1876:386 (type locality: Colon, Panama).

Poecilia cuneata Garman, 1895:179, plate V (type locality: Colombia, Gulf of Uraba, Turbo); *Poecilia sphenops cuneata*; Hubbs, 1926b:77.

Poecilia salvatoris Regan, 1907:65, plate 14, figs. 2–3 (replacement name for *P. thermalis* Günther, 1866).

Platypoecilus tropicus Meek, 1907:146 (type locality: Costa Rica, Turrialba).

Poecilia tenuis Meek, 1907:147 (type locality: Costa Rica, Tiribi).

Poecilia caudata Meek, 1909:209–210 (type locality: Costa Rica, Turrubares).

Poecilia spilonota Regan, 1908:460 (type locality: San José, Costa Rica).

Lembesseia parvianalis Fowler, 1949:267–269 (type locality: Africa, Congo system, Oka).

Mollienesia sphenops petersi Schindler, 1956:1–4, fig. 1 (type locality: Honduras, lake Yojoa).

Material.—Nicaragua: Lectotype of *P. dovii* (BMNH 1863.12.16.77, Lake of Nicaragua, coll. captain J. W. Dow, no date). 5 Paralectotypes of *P. dovii,* (BMNH 1863.12.16.78-92, same data as BMNH 1863.12.16.77).

Costa Rica: 4 Syntypes of *P. spilonota* (BMNH 1907.2.11.44-50, San José, coll. P. Bidley, no date).

Panama: NWM 21608 (1 syntype of *Xiphophorus Gillii*), Rio Chagres, Panama, no further data. MCZ 29433 (10), 1 mile south of Panama City, coll. USFC Steamer Albatross (Alex. Agassiz), 23-X-1904; MCZ 33847 (10), ca. 9°43′N, 79°43′W, be-

tween Gorgona and Matachin, collected before 1930; MCZ 54068 (10), small tributary of main stream on left about 0.75 km upriver of bridge, Bayano drainage, probably Rio Canita, Panama, coll. W. L. Fink & K. E. Hartel, 1-IV-1978; USNM 050368 (14), Panama, coll. C. H. Gilbert; USNM 64764 (17), Folks R. Swamp, Cristobal, coll. A. H. Jenning, 4-VIII-1909; USNM 65618 (15), 1 mile south of Panama city, coll. Str. Albatross, 23 X-1904; USNM 78837 (27), Upper Trinidad, coll. Meek & Hildebrand, 7-III-1911; USNM 247529, (24) canals in banana field, Bocas Province, California, coll. Loftin, 2-IX-1962; USNM 247531, (44) Rio Gaurumo, Bocas Province, coll. Loftin, 18-IV-1963; USNM 247432 (10 of 50), Canal zone, behind Fort Clayton, residential area, coll. Loftin & Tyson, 19-IV-1962; USNM 247436, (6) Bocas del Toro, Esendo de Verequas island, coll. J. Legler, 14-V-1962; USNM 247548, (35) San Blas, small river opposite to Mulatupo island, coll. Loftin & Evermann, 2-XII-1962; USNM 247550, (18) San Blas, Rio Acla, coll. Loftin, 16-XII-1962; USNM 293473, (10 of 51) 9°14′N, 78°58′W, Rio Tearbles, Bayano drainage, Panama province, coll. W. C. Sternes et al., 25-II-1985; USNM 293476, (23) 9°28′N, 79°3′W, Comarca Kuna Yala, Rio Mandinga, coll. W. C. Sternes et al., 5-III-1985; USNM 293494 (42), Panama province, Rio Frijoles, above pipeline rd., N. of Gamboa (Rio Chagres drainage, Atlantic side), coll. W. C. Sternes et al., 26-II-1985.

Colombia: 2 Syntypes of *P. cuneata* (MCZ 6458, Turbo, Gulf of Uraba, Colombia, coll. T. Barbour, no date); 3 Syntypes of *P. cuneata* (USNM 120285, same data as MCZ 6458); 5 Syntypes of *P. Boucardi* (MCZ 32959, San Pablo (Aspinwall (Colon), Quebrada San Pablo), coll. Hassler Expedition (Steindachner & Mr. Boucard), VII-1872); BMNH 99.3.15.27-29 (3), Monkey Hill, Colon, coll. Dr. H. Festa, no date.

Additional material from Nicaragua and Panama in Poeser (1992), from El Salvador in Poeser (1995).

Diagnosis.—A = 9; D = 9–10; CPS = 16; LLS = 26–29. In his checklist, Miller (1983) was uncertain if *P. gillii* was different from *P. mexicana*. Therefore, I have included a discussion of this species in the remarks section.

Description.—This species is very similar to *P. mexicana*, with the exception of the number of scales around the caudal peduncle. In *P. mexicana*, 18 scales around the caudal peduncle are common.

Remarks.—All examined type material is consistent with the above meristic data. Over its extensive range, *P. gillii* shows considerable variation in body shape and in dorsal fin color, and moderate variation gonopodial features. These variations appear to reflect intraspecific diversification, justifying taxonomic separation, i.e., division in subspecies. Carr & Giovannoli (1950:17–18) reported the live colors of *P. gillii* and the sympatric *P. marcellinoi* Poeser, 1995 from Honduras: "One male with yellow spots, a black blotch at the caudal base and spotted dorsal and caudal fin, and one female with black spotted sides (=*P. marcellinoi*). One female with yellow spotted sides, and a male with golden-orange blotches, with a black blotch on the dorsal base and rest of fin orange (=*P. gillii*)."

Poecilia gillii salvatoris is reported from El Salvador, where males from most populations are reported to have red dorsal fins (Hildebrand 1925). This prompted Miller (1994) to redescribe *P. salvatoris* Regan, 1907, although all other characters are as found in the present study for *P. gillii*. Poeser (1995) in his redescription of *Poecilia salvatoris* agreed with the diagnosis of *P. salvatoris* by Regan (1908), with the exception of the number of anal fin rays. Regan (1908:104) mentioned 8–9 anal fin rays; however, examination of 14 of his syntypes did not yield any specimen with eight anal fin rays, so Regan's account is judged erroneous. In the preserved material, no trace of red was found in the dorsal fins. The red finned western Central American popula-

tions are here considered as a subspecies, viz., *P. gillii salvatoris*.

Villa (1982) provided a key to the genus *Poecilia* in Nicaragua, in which he recognized three species, viz., *P. gillii, P. sphenops*, and "an undescribed species with unicuspid teeth". He mentioned (p. 134, translated from Spanish):

P. gillii: "Unicuspid inner teeth, incomplete supraorbital system, preorbital pores free, 26–28 (modally 27) lateral scales, 16 scales around caudal peduncle, 28–30 (modally 30) vertebrae. Guatemala, El Salvador, to Panama".

P. spec.: "Unicuspid inner teeth, complete supraorbital system, free preorbital pores, 28–30 (modally 29) lateral scales, 18 scales around caudal peduncle, 28–30 (modally 30) vertebrae. Rio Ulya (Honduras), Lagunas Apoyeque and Xiloa, lake Managua and Nicaragua, and Rio Sapoa & Frio, Tilaran region, Costa Rica".

P. sphenops: "Tricuspid inner teeth, incomplete supraorbital pores, preorbital pores covered, 26–28 (modally 27) lateral scales, 16–18 scales around caudal peduncle, 28–30 (modally 29) vertebrae. Guatemala and El Salvador, Atlantic side of Honduras, Nicaragua including the Great Lakes".

Villa's diagnosis of *P. sphenops* fits the description of *P. marcellinoi* (tricuspid inner teeth, 16 scales around the caudal peduncle). While his description of *P. gillii* is accurate, his figure of *P. gillii* shows 9 transverse scales on the caudal peduncle, which is a diagnostic character of *P. mexicana*. I suspect the figures were switched. His undescribed species might very well be *P. mexicana*. The apparently aberrant number of lateral scales (also mentioned by Bussing [1987]) is explained by character displacement (cf. Poeser 1995). The only synonym of *P. sphenops* in Rosen & Bailey (1963) from Nicaragua is *P. dovii* Günther, 1866. *Poecilia dovii* was considered synonymous with *P. sphenops* by Regan (1908). Since the type material of *P. dovii* contained specimens from *P. mexicana* (with 18 scales around the caudal peduncle), as well as from *P. gillii* (with 16 scales around the caudal peduncle), it is only partially alluded to the synonymy of *P. gillii*. In honor of captain J. W. Dow, the lectotype is selected from the lot he collected himself in Nicaragua, which is *P. gillii*. Günther (1866) mentioned that *P. dovii* occurred only in Guatemala and Mexico. However, since the type locality includes Nicaragua, this country should be included in the range of distribution. The specimens from Lake Amatitlàn (BMNH 1865.6.10.13-15) are not registered in the British Museum as syntypes, and these were not studied. The specific status of these types remains to be determined.

Poecilia gillii appears to be nearly the only species of *Poecilia* present in Costa Rica. Meek (1914:116–117) placed all Costa Rican taxa in synonymy with *Platypoecilus tropicus* (=*P. gillii*) as follows: "The inland or fresh-water forms of this species or variety found in Costa Rica are very variable, and as a result several species have from time to time described. . . . The females and many males of these inland forms usually have a black spot at the base of the middle dorsal rays, ... On many specimens from salt and brackish water some of the scales have a dark spot which forms lines along the rows of scales. . . . On many of the males, especially from larger streams, the basal half of the caudal is black, or with black blotches; on some of these the basal half of the dorsal is also black." Specimens with a black basal half of the caudal fin, formerly described as *P. caudata* Meek, 1909, are herein recognized as a subspecies, viz., *P. gillii caudata*.

Bussing (1987) identified most of the Costa Rican populations as *P. gillii*. He gave the following description (translated from Spanish): "Body with yellow spots, in some females these spots are black. Scales in a lateral series 26–28, mostly 27. Three orbital pores in one line. In the males sometimes a large dorsal fin, with black spots or

blotches at the base. Caudal fin with spots, blotches or solid black pigmentation. Some males with orange in their caudal fin. Other fins yellow, head and body bluish. Note: some males have a red dorsal. Large species, up to 105 mm." Males possessing a red dorsal fin are *P. gillii salvatoris.* Bussing also recorded *P. mexicana,* in a much lower frequency, i.e., three populations from over fifty in total, widely apart from each other (Bussing 1987:144, map 20). His diagnosis for this species is: "Very much like *P. gillii.* Yellow spots on body, black in some females. 28–30 (modally 29) Lateral scales, and three orbital pores, forming a triangle. Dorsal and caudal spotted, rest of fins yellow. It is also a large species, up to 110 mm." Bussing (1987) illustrated *P. gillii* and *P. mexicana* in his paper, and his diagnoses of *P. gillii* and *P. mexicana* correspond with the account of Villa (1982) (see above). Surprisingly, Bussing did not record any populations of *P. marcellinoi.*

Hubbs (1926, 1953) considered *P. sphenops* in Panama either *P. sphenops cuneata* (cf. Hubbs 1926), or *P. s. gillii* (cf. Hubbs 1953). Examination by me of Panamanian populations confirms earlier findings of profound morphometric differences, as well as constant meristic data, in all Panamanian populations. A conspicuous reduction of the gonopodial spine on ray 5 is noted. In populations near the Costa Rican border (Bocas del Toro district of Panama) the spine is distinct. In populations near Colombia, i.e., the San Blas area, it is reduced or absent, as is found in *P. koperi* (Fig. 4a). This shift in character expression from west to east is not accompanied by meristic changes.

Although some populations contain poorly pigmented, slender specimens, other populations manifest heavily pigmented, stout specimens. Nevertheless, all specimens have nine anal fin rays, nine (or rarely ten in the San Blas district) dorsal fin rays, 16 scales around the caudal peduncle, 18 scales around the body, and 26 to 29 scales in a lateral series. The consistency of these counts suggests that all populations belong to the same species.

Because the missing spine is of taxonomic significance, this form was named *P. gillii cuneata* Garman, 1895. The populations of *P. gillii* from Panama examined in the present study are partly sympatric with *P. marcellinoi* like in El Salvador (Poeser 1995). Poeser (1992) reported a male with an aberrant gonopodium from Nicaragua (GCRL 6697), identified then as *P. mexicana mexicana.* Re-examination of my notes proved that the identification and locality was wrong. The sample containing this male was GCRL 8748, viz., *P. gillii cuneata* from Panama.

Rosen & Bailey (1963) considered *Lembesseia parvianalis* a synonym of *P. sphenops.* However, since *L. parvianalis* has unicuspid inner teeth, Miller (1983) placed it in the synonymy of either *P. mexicana* or *P. gillii.* Based on the original description, in which 8 transverse scales on the caudal peduncle are illustrated, I assign it to the synonymy of *P. gillii.* Fowler's (1949) record is important for its taxonomic value. The *P. sphenops* group, if raised to generic level, would become *Lembesseia* (with *L. surinamensis* (=*P. sphenops*) as type species).

Distribution.—Poecilia gillii is recorded from the Pacific coast of Guatemala to the Atlantic coast of Colombia. In northern regions, from Guatemala to Costa Rica, it is represented by the subspecies *P. gillii salvatoris.* The subspecies *P. gillii caudata* occurs in Costa Rica, whereas *P. gillii gillii* is present in Panama. The South American populations, as well as adjacent populations in Panama, are considered to be *P. gillii cuneata.* The type locality of *P. cuneata* was designated "Turbo, Gulf of Darien" (Garman 1895). Rosen and Bailey (1963) added 'Panama' to this locality. However, study of several maps did not confirm this addition. The nearest village with that name is near the Gulf of Uraba, an extension of, and sometimes also so-called, the Gulf of

Darien, in Colombia. I presume that this is the correct type locality.

Poecilia caucana (Steindachner, 1880)

Girardinus caucanus Steindachner, 1880: 87, plate 4, figs. 4, 5 (type locality: Colombia, Caceres); *Allopoecilia caucana* Hubbs, 1924:11.

Material.—Colombia: UMMZ 186317 (51), Depto. Cordoba, Tierra Alta, Rio Sinu, coll. W. Moberley & K. Adler, 1965.

Venezuela: UMMZ 186931 (54), Rio Monay, coll. F. F. Bond, 1938; UMMZ 186934 (24), Quebrada Goajira, F. F. Bond, 1938; UMMZ 186937 (44), Rio Bucares, coll. F. F. Bond, 1938; USNM 86264 (4), Valera, Trujillo, coll. H. Pitteir, 1923; USNM 121677 (33), Rio Motatan, 4 km above Motatan, coll. L. P. Schultz, 25-III-1942.

Panama: USNM 293444, (7), Rio Meteti, Darien Province, 40 km NNW of Yaviza, coll. W. C. Sterns et al., 24-II-1985; USNM 293574, (10), Rio Peresinico, Darien Province, coll. B. Chernoff, J. Lundberg, L. McDade, 23-II-1985.

Diagnosis.—A = 8; D = 7–8; C = 18–22; LLS = 26–27; CS = 16; CPS = 14. *Poecilia caucana* is a small to medium sized species, characterized by a black band in its dorsal fin. The gonopodium has ray 4p with broader rays than ray 4a.

Description.—This is one of the smaller species of the genus. The largest specimens examined are a female of 37.4 mm SL and a male of 27.2 mm SL. The dorsal fin has a black transverse band at the base. This fin is usually milky white or yellow, although also red fins are reported in aquarium literature. The other fins are unmarked.

The gonopodial characters figured in Rosen and Bailey (1963) are of considerable interest because gonopodial ray 4p is thicker than ray 4a. In addition, the hook on gonopodial ray 5 is weakly developed.

Distribution.—Atlantic slopes of Panama, Colombia and Venezuela.

Poecilia vandepolli van Lidth de Jeude, 1887

Poecilia Vandepolli van Lidth de Jeude, 1887:137, Pl. 2, Figs. 4 and 5 (type locality: Curaçao).

Poecilia Vandepolli arubensis van Lidth de Jeude, 1887:138, Pl. 2, Figs. 6–10 (type locality: Aruba).

Lectotype.—Curaçao: RMNH 5155, adult male, Curaçao, coll. Neervoort and v. d. Poll, no further data.

Paralectotypes.—RMNH 33843 (4), same data as RMNH 5155.

Material.—Aruba: RMNH 5156 (6 syntypes of *P. Vandepolli arubensis*), Aruba, coll. Neervoort and v. d. Poll, no further data. See also tables below, details in Poeser (1992).

Diagnosis.—A = 8–9; D = 7–8; C = 16; LLS = 26–27; CPS = 16. Several specimens have humeral blotches anterior to the position of the lateral side spot as occurs in *P. vivipara.* The gonopodium lacks extrusions on ray 3 and 5p.

Description.—Poecilia vandepolli is reported to have specimens with orange on the ventral side of the body, yellow specimens with blue sides and grayish brown specimens in the same population (Feltkamp and Kristensen 1969). Speckled specimens, allegedly only occurring in Venezuelan populations (Feltkamp and Kristensen 1969), also appear on Curaçao. The pigmentation at the base of the dorsal fin forms a blotch, in addition to dark spots. The body may have a humeral blotch, positioned more anteriorly than a similar such patch of color in *P. vivipara.* The females tend to be paler than males.

The gonopodium, figured in Poeser (1992), is like that of *P. vivipara,* with the exception of the serrae on ray 4a. When fully developed, a little membranous bulge is found on gonopodial ray 3, which covers extruding serrae.

Description of the types.—The lectotype is a mature male, 27.3 mm SL. It has 8 dorsal fin rays and 16 scales around the

caudal peduncle. Several scales in the lateral series are missing on this specimen and the caudal fin is damaged, so no further meristic data can be given. Gonopodial ray 3 has a long terminal segment, the hood is short. An extremely short extrusion similar to a small hook is present. Gonopodial ray 4a is unmodified, ray 4p has eight unmodified distal segments followed by serrated segments. Gonopodial ray 5a is one segment longer than 5p. Subdistal ventral modifications occur on ray 5a. The largest female paralectotype, 47.5 mm SL, has about 25 scales in a lateral series (this number is not accurate because some scales are missing). It has nine dorsal fin rays and nine anal fin rays, the caudal fin is damaged.

The specimens in the type series from Aruba are much smaller. The largest male, 22.0 mm SL, has a gonopodium like the lectotype, with seven distal unmodified segments on gonopodial ray 4p and no trace of a hook on ray 3. It has 8 dorsal fin rays, 16 scales around the caudal peduncle, and about 24 scales in a lateral series (some scales are missing). The caudal fin is damaged. This male has a pigmented band proximally on the dorsal fin and a pigmented humeral blotch. The largest female (26.5 mm SL) has eight anal fin rays and nine dorsal fin rays. The caudal fin is damaged. Sixteen scales are found around the caudal peduncle and 27 in a lateral series.

To establish morphometric and meristic variations a detailed examination of 15 populations was carried out. Some 12 lots were examined from Aruba, and three lots from Curaçao (Table 1).

Distribution.—*Poecilia vandepolli* occurs naturally in all kinds of waters of the Netherlands West Indies (Aruba, Curaçao, and Bonaire). It is introduced on St. Maarten/St. Martin (Poeser 1992).

Poecilia koperi, new species
Fig. 1, Table 2

Poecilia vivipara (non Bloch & Schneider, 1801); De Beaufort, 1940:111.

Poecilia sphenops (non Valenciennes, 1846); Regan, 1913:1013 (in part).

Poecilia sphenops vandepolli (non Van Lidth de Jeude, 1887); Schultz, 1949:84, 97–99 (in part).

Poecilia sphenops cuneata (non Garman, 1895); Hubbs, 1926:77.

Holotype.—Adult male, UMMZ 223343, Venezuela, Rio Curipe at Higuerote, coll. F. F. Bond, 2-V-1938.

Allotype.—Adult female, UMMZ 223344, same data as UMMZ 223343.

Material.—BMNH 1909.2.25: 53-56 (5), Venezuela, coll. Arnold, no date; UMMZ 200738 (15 of 123), 2 km N of Ocumare, lagoon on flats near mouth of Rio Cumboto, coll. F. F. Bond, 5-I-1938; UMMZ 200740 (15 of 57), Rio Guaiguaza, 3 km W of Porto Cabello, 2 km from mouth of river, coll. F. F. Bond, 15-I-1938; UMMZ 200744 (12), Rio Sanchon, 5 km W of Tavorda, 10 km W of Porto Cabello, coll. F. F. Bond, 26-I-1938; UMMZ 200753 (15 of 430), Lagunita, 5 km W of Coro, Estado Falcon, coll. F. F. Bond, 19-III-1938: UMMZ 200755 (15 of 115), Falcon, Laguna del Rio Capatárida, at mouth, 5 km N of Capatárida, coll. F. F. Bond, 2-III-1938; UMMZ 200760, (15 of 152), Falcon, Coastal lagoons, 15 km N of Maracaibo, coll. F. F. Bond, 6-IV-1938; UMMZ 200761 (13 of 202), same data as UMMZ 223343; UMMZ 200762 (15 of 80), Estado de Miranda, Lagunita de Tacarigua, at Tacarigua, 85 km E of Caracas on the coast, near the boca, coll. F. F. Bond, 3-II-1939; UMMZ 200764 (28), Boca del Rio Cumboto, 2 km NW of Ocumare; ZMA 109.206 (6), La Goajira, Rio Calancala, San Antonio, coll. P. Wagenaar-Hummelinck, 17-I-1937; ZMA 119.909 (30), Paraguana Estangue de Moruy, coll. P. Wagenaar-Hummelinck, 18-II-1937; ZMA 119.910 (15), Paraguana, Estangue de Santa Ana, coll. P. Wagenaar-Hummelinck, 16-II-1937; ZMA 120.885 (4), 2 km N of Barcelona, Rio Guanta, coll. P. Wagenaar-Hummelinck, 1936.

Table 1.—Overview of standard lengths, proportional measurements and meristic data of *Poecilia vandepolli.*

	SL	Pred	CPd	A	D	C	LLS	CPS
Aruba								
ZMA 100.600. The fish were caught in a small freshwater stream, Rooi Prins at 'Plantage Fontein'. The lot contains small specimens, of which the largest male (20.7 mm SL) has an unclear humeral spot. The gonopodium of this male is fully developed. The bodies are olive brown, without any additional pigmentation. Dorsal fin pigmentation lightly spotted, darker in males than in females. (Three additional small males are without a humeral blotch.) Eight females (22–31 mm SL), eight subadults and 30 juveniles complete this lot.								
Males	19.4	575	175	—	8	16	25.5	15
Females	26.0	610	156	8.8	7.5	15.8	26.1	15.6
ZMA 100.606. This lot was collected in a freshwater pool at 'Plantage Fontein'. It contains medium sized specimens, largest males about 35 mm SL with a clear humeral blotch (at scale 5 of LLS) and a large dorsal fin that reaches the base of the caudal fin. The dorsal fin has a large anterior blotch at the base. In this lot there is a total of six males with humeral blotch, all adults, of which two males do not possess a blotch, 14 females (30-48 mm SL), eight subadult and 30 juveniles.								
Males	34.6	551	207	—	8.3	18	26.3	16
Females	43.3	613	173	9	8	16.4	26.5	16
ZMA 100.607 is a sample from a small pool of freshwater at 'Fontein Plantage'. Only one fully grown male (without blotch) is present, with one fully grown female. It further contains three subadults and five juveniles.								
Male	33.6	533	162	—	8	17	25	16
Female	41.9	616	159	9	8	17	27	16
ZMA 100.608, again from a small freshwater pool at 'Fontein Plantage'. Two males in this sample have a blotch, viz., the largest and the smallest males. One male is without blotch. One large female is present, together with one small female. 12 Juveniles.								
Males	30.9	581	200	—	8	17	26.3	16
Females	34.0	611	170	9	8	16	27	15
ZMA 102.212. Pool at the well 'Rooi Prins'. Males in this lot have faded humeral blotches. The largest males have the dorsal fins to caudal base, with an anterior blotch at the base.								
Males	30.6	588	180	—	8	16	26	16
Females	33.1	653	171	9	7.8	18	26	15.7
ZMA 120.413. 'Spaans Legioen'. 54 Small, dark specimens, of which 22 are males, 25 are females, six subadults and one juvenile. No characteristic coloration can be observed. Dorsal fins and anal fins are damaged.								
Males	23.7	602	184	—	—	17.7	26.3	16
Females	26.4	607	177	—	—	16	25.7	15.7
ZMA 120.414. This lot is from 'Rooi Awa Marga', which is a slow stream. One small male with a completely developed gonopodium is present, with five small females and five juveniles.								
Male	16.0	563	163	—	8	16	25	16
Females	21.6	602	153	8	7	16.5	25.5	16
ZMA 120.415. Salinja master, caught at an abandoned saltpan (24 g Cl/l). The sample contains five males, three females, three subadults and 3 juveniles. The scales of these specimens are white and hard, probably caused by the high salinity.								
Males	24.7	633	167	—	8	16	26	16
Females	25.8	627	149	9	7.5	15.5	26	16
ZMA 120.422. Salinja master, east. Again the abandoned saltpan (6 g Cl/l). Nine males, of which the two largest were very dark. These two specimens are not recorded in the table. 19 Females are found, of which one has many irregularly positioned spots. Eight subadults and four juveniles complete this lot.								
Males	22.8	598	172	—	8	16	26	16
Females	23.3	638	149	8.7	8	15.7	26.5	15.8
ZMA 120.423. 'Bron Rooi Prins' pool. It contains sixteen males, twenty-three females and 4 subadults.								
Males	31.0	606	187	—	8	16	25.3	16
Females	35.8	627	172	9	8	18	25.8	16

Table 1.—Continued.

	SL	Pred	CPd	A	D	C	LLS	CPS
ZMA 120.425. 'Salinja Balashi'. 9 Males, fifty-eight females, eighteen subadults and 2 juveniles. This population has some extra-ordinary features. The population consists of more or less colorless specimens. The males are few in number, and one specimen seems of intermediary sex, i.e., does not have his gonopodium fully developed while being large enough. The other eight males are normally developed. Many females only have eight anal fins.								
Males	22.0	562	187	—	8	16	25	16
Females	29.3	616	169	8.3	7.8	16.6	26.3	16
ZMA 120.437. 'Fontein pond'. Seven males, six females, five subadults and one juvenile.								
Males	32.5	577	190	—	7.7	16.7	25.7	16
Females	27.5	626	144	9	8	16.7	27.5	16
Curaçao								
ZMA 100.603. Zaquito. A note in bottle reads: males with orange-red dorsal fins, orange-red gill-areas, ventral sides and caudal fins. On the sides 3 to 6 rows of orange-red spots.								
Males	30.7	510	168	—	8	16	25	14.5
Females	29.7	622	163	8.2	7.8	16	25.8	15
ZMA 123.465. 5 km SWS of Willemsstad, from a tidal pool. The complete population was poisoned, and contains more males than females. 48 Males, of which some have more than one humeral blotch. All males are heavily pigmented, i.e., are speckled. Some have rows of black spots on the caudal peduncle. 36 Females, 3 subadults, 1 juvenile.								
Males	38.4	506	171	—	8	16	26.3	17.5
Females	39.4	581	155	8.9	7.9	16	26.6	16.9
ZMA 123.466. Hato. 127 mainly black or dark brown specimens.								
Male	31.3	474	180	—	8	16	26	17
Females	30.2	674	164	8.5	8	16	25.5	16
Averages of Morphometric and Meristic Data								
Aruba								
Males	26.8	580.8	181.2	—	8.0	16.5	25.7	15.9
Females	30.7	620.5	161.8	8.8	7.8	16.5	26.3	15.8
Curaçao								
Males	33.5	496.7	173.0	—	8.0	16.0	25.8	16.3
Females	33.1	625.7	160.7	8.5	7.9	16.0	26.0	16.0

Colombia: BMNH 1899.3.15: 24-26, (2), Colombia, coll. H. Festa, no date.

Diagnosis.—A = 8 (rarely 9); D = 8 (rarely 7); LLS = 25–26; BS = 18; CPS = 16; PS = 11–13

Descriptions.—*Poecilia koperi* has unicuspid inner teeth. The largest specimens examined are a female of 56.2 mm SL and a male of 47.0 mm SL.

Holotype.—The largest male (38.5 mm SL) has a deep body, with depressed sides. The upper part of body exhibits two dark horizontal rows of dark spots, which are less conspicuous ventrally. The body is brown, dorsally darker than ventrally. The caudal fin has black spots on the membrane between the rays. The dorsal fin is pigmented like caudal fin, reaching caudal base. The inner jaw dentition is unicuspid. Proportional body measurements in Table 2.

Meristic data include 26 scales in the lateral series, 12 predorsal scales, 16 scales around caudal peduncle, and 18 scales around body. Pectoral fins exhibit 16 rays, the dorsal 8 fin rays, and the caudal 17 fin rays. The last segment of gonopodial ray 3

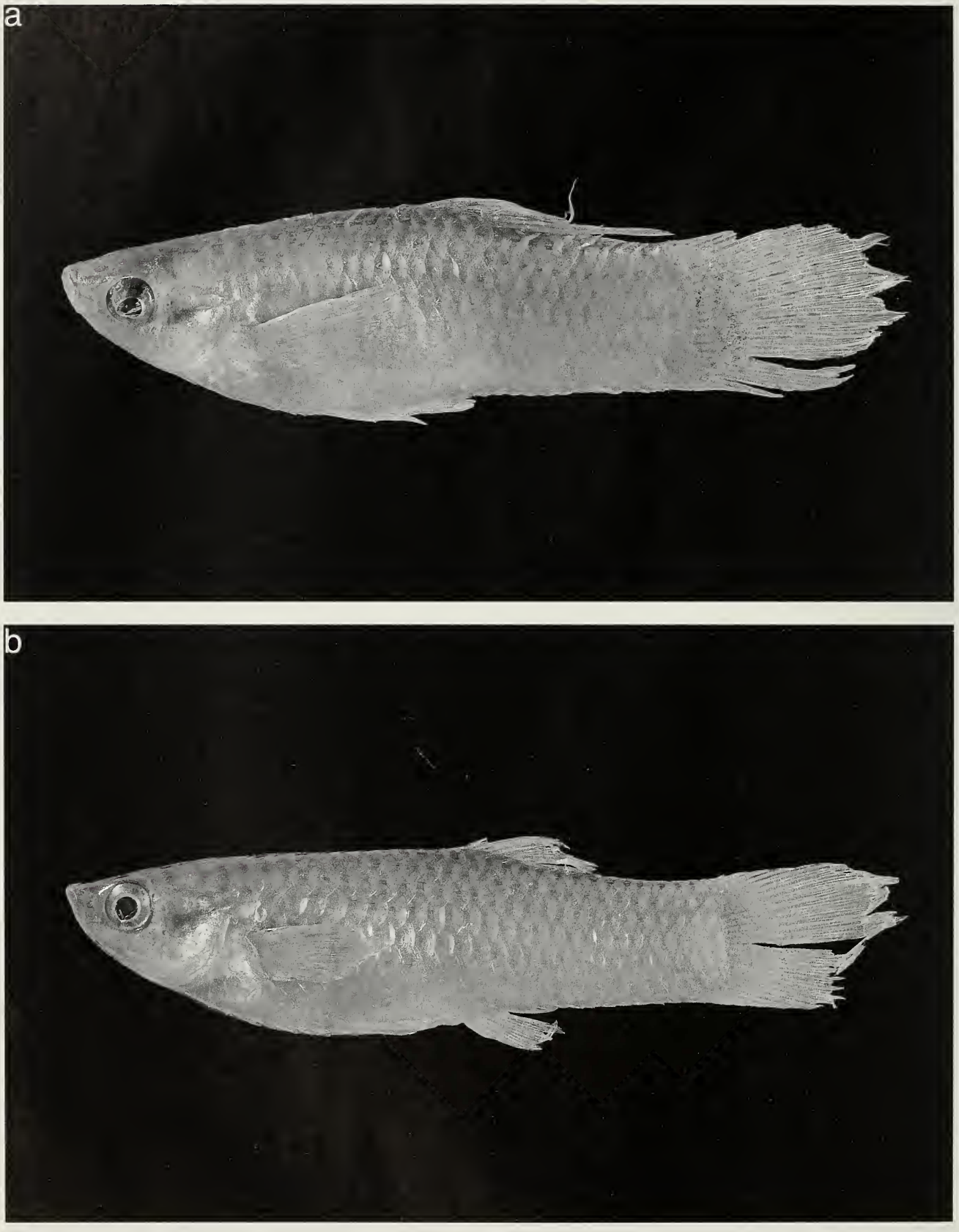

Fig. 1. *Poecilia koperi,* (a) holotype, (b) allotype.

has an extruding spine, two subsequent segments without serrae, nine segments with ventral processes, and the other segments with serrae on both sides (Fig. 4a). Ventrally on ray 3, a hood is present, not reaching the tip. Ray 4a of the gonopodium is without serrae, ray 4p has ten distal unserrated segments, followed by ten segments

Table 2.—Proportional measurements of *P. koperi, P. boesemani* and *P. wandae.* The standard lengths are in millimeters, proportional measurements in thousandths of the standard length.

	Poecilia koperi				*Poecilia boesemani*		*Poecilia wandae*			
	Males	(Holotype)	Females	(Allotype)	(Holotype)	(Allotype)	Males	(Holotype)	Females	(Allotype)
Standard Length (mm)	34.8	38.5	34.1	40.6	43.8	47.8	20.4	18.1	19.9	23.1
Predorsal Length	543	535	592	579	573	586	577	582	606	636
Dorsal Origin to Caudal Base	396	463	294	351	397	402	389	390	371	342
Anal Origin to Caudal Base	495	562	303	346	534	368	549	522	358	381
Body Depth	281	348	214	253	320	326	269	253	270	273
Head Length	242	253	198	219	228	243	243	286	278	199
Head Width	167	191	144	171	210	222	170	165	181	173
Caudal Peduncle Length	468	553	266	282	486	276	530	527	392	312
Caudal Peduncle Least Depth	198	253	138	164	192	174	187	187	158	165
Interorbital Bony Width	132	146	114	134	137	132	114	110	127	126
Mouth Width	92	110	76	84	110	111	74	60	88	91
Snout Length	38	48	29	39	41	50	—	—	—	—
Orbital Length	60	59	48	50	62	56	—	—	—	—
Dorsal Fin Depressed Length	361	452	156	—	295	238	205	220	166	147
Dorsal Fin Basal Length	131	163	80	96	151	138	—	—	—	—
Anal Fin Depressed Length	200	202	126	144	221	157	267	308	179	177
Anal Fin Basal Length	—	—	53	57	—	67	—	—	—	—
Pectoral Fin Length	160	253	160	182	212	195	—	—	—	—
Pelvic Fin Length	96	185	166	105	180	123	229	264	—	117
Caudal Fin Length	215	371	214	239	253	236	—	330	—	173

with dorsal serrae. Rays 5a and 5p do not have spines, and are seven segments shorter than 4p.

Allotype.—The largest female (40.6 mm SL) has spots on the body like those of the holotype, and has fins with indistinct pigmentation. The dorsal fin is short, reaching halfway from the base of the first ray to the caudal fin base. The caudal fin has 16 rays, the anal fin has eight rays. The other meristic counts are like those in the holotype.

Distribution.—*Poecilia koperi* occurs in coastal areas from the Peninsula de Araya, Venezuela to the eastern part of Colombia.

Etymology.—This species is named after my friend Michel Koper, with whom discussions have helped to keep my thinking flexible.

Remarks.—*Poecilia koperi* is a medium sized species of the *Poecilia sphenops* complex (cf. Miller 1983), distinguished from *P. gillii cuneata* only by the reduced number of fin rays in the dorsal and anal fin. From the other subspecies of *P. gillii* it is distinguished by gonopodial characteristics.

Two geographically separated color morphs exist in this species. The pigmentation of the body of specimens east of Coro consists of two or three horizontal rows of spots, which are less conspicuous ventrally. The body becomes darker dorsally, as opposed to the lighter ventral side. The unpaired fins are moderately pigmented, i.e., they only have spots on the membrane between rays. The dorsal fin reaches to the base of the caudal fin. The populations west of Coro, i.e., in the Maracaibo basin, are more intensely pigmented. The males have about 10 distinct vertical stripes from halfway the body to the caudal base. The scales on the body have pigmented margins. The base of the caudal fin is covered with scales, which are irregularly pigmented. The caudal fin has longitudinal spots, the dorsal fin has a median blotch from the base to halfway the fin, distally replaced by dark spots. The females are pigmented like the males, but with fainter stripes on the body. The fins in the females are without spots and the snout is less pointed. Meristic data and the gonopodium are identical in the two populations, although Maracaibo populations never have seven dorsal fin rays, nor nine anal fin rays. The gonopodium has a fleshy hood that nearly reaches the tip. Gonopodial ray 3 has two or three weakly serrated terminal segments. Other segments of ray 3 have ventral serrae and irregular dorsal extrusions. A membranous ventral hook is found on the edge of the last segment. Gonopodial ray 4a is with long unserrated segments. Gonopodial ray 4a possesses seven to eleven unserrated distal segments, others segments have dorsal serrae. This ray is somewhat shorter than ray 4a. Gonopodial rays 5a and 5p have long unserrated segments ending at fourth to seventh segment of ray 4p counting from the tip (Fig. 4a).

Schultz' (1949:97) record of *P. vivipara,* partly based on de Beaufort's (1940) account, is erroneous; re-examination of the specimens mentioned by de Beaufort (1940: 111) in ZMA revealed that this material is *P. koperi.*

Poecilia boesemani, new species
Fig. 2, Table 2

Poecilia sphenops (non Valenciennes, 1846); Regan, 1913:1013 (in part); Price, 1955:18; Boeseman, 1960:122.

Holotype.—RMNH 21543, adult male, Trinidad, Port of Spain, Maraval River, coll. M. Boeseman, 27-VII-1954.

Allotype.—RMNH 32428, adult female, same data as RMNH 21543.

Diagnosis.—A = 8; D = 8–9; LLS = 27; BS = 20; CPS = 16; PS = 13–16.

Description.—Holotype: male, 43.8 mm SL. The body does not have a distinct pattern of pigmentation. The dorsal fin is angular, with dark spots on the membranes between the rays. These spots form two regular horizontal lines. In the caudal fin, a vertical line of similar spots is found on the posterior part. Proportional body measurements in Table 2.

Fig. 2. *Poecilia boesemani,* (a) holotype, (b) allotype.

The dorsal fin has 10 rays, the caudal fin has 18 fin rays. Pectoral fin with 16 rays, 20 scales around the body, 16 scales around the caudal peduncle, 27 scales in a lateral series. The holotype misses one or two predorsal scales, so the exact number is unknown. All head pores are exposed. The gonopodium is like *P. mexicana* (Fig. 4b, see Miller 1975), i.e., with a spine in the membranous hook on gonopodial ray 3. In-

ner jaw teeth unicuspid or possibly subtricuspid (Garman 1895, Miller 1975).

The female allotype is 47.8 mm SL. The morphology and pigmentation are like that noted in the holotype but without spots in the caudal fin. The anal fin has 8 rays, the dorsal fin contains 9 rays, the pectoral fin has 13 rays. All other counts are identical to those of the holotype.

Distribution.—This species is known only from its type locality.

Etymology.—This species is named after Dr. Marinus Boeseman, emeritus curator of the ichthyological collection of the National Museum of Natural History, Leiden (RMNH), who collected the specimens.

Poecilia wandae, new species
Figs. 3, 4, Table 2

Holotype—USNM 121683, adult male, Venezuela, Maracaibo basin, hot spring, creek tributary to Rio Mechango, 20 km above bridge, coll. L. P. Schultz, 21-III-1942.

Allotype.—USNM 326142, adult female, same data as USNM 121683.

Material.—USNM 121669 (4), Cano, ½ mile W of Sinamaica, coll. L. P. Schultz, 11-III-1942; USNM 121670 (3), Rio Socuy, 3 km above mouth, coll. L. P. Schultz, 24-II-1942; USNM 121671 (42), Cienago del Guanavana, about 10 km N of Sinamaica, coll. L. P. Schultz, 11-III-1942; USNM 121672 (12), Rio San Juan, 12 km S of Rosario, coll. L. P. Schultz, 26-II-1942; USNM 121673 (1), Rio San Ignacio, about 20 km S of Rosario, coll. L. P. Schultz, 26-II-1942; USNM 121674 (1), Rio Negro, below mouth of Rio Yasa, coll. L. P. Schultz, 2-III-1942; USNM 121675 (27), Lago Tule, about 75 km W of Maracaibo, coll. L. P. Schultz, 1-III-1942; USNM 326143 (261), same data as USNM 121683.

Diagnosis.—D = 5–7; A = 6–8; C = (probably) 14–16; LLS = 24–26; PS = 11–13; BS = 16; CPS = 14. This species is very much like *P. caucana,* differing only in regards to the reduced meristic and gonopodial characteristics.

Description.—*Poecilia wandae* is a small species, with mature males ranging from 13 to 22 mm SL. Most specimens have a brownish body with 7 to 10 vertical stripes extending from the caudal peduncle to halfway along the body. In some specimens a longitudinal stripe over the lateral line is present. The dorsal fin has a median basal blotch and a black margin, whereas the other fins are unmarked. *Poecilia wandae* has an elongated body with a compressed head. Females have fewer vertical stripes than the males. Gonopodial ray 3 at the tip with 1 or 2 unserrated elements, all other segments of this ray are serrated on both sides (Fig. 4c). The fleshy hood reaches the tip. Gonopodial ray 4a has long, unserrated segments, with the last segment pointing downwards, while 4p has 7–8 square unserrated elements at the tip and the distal segment pointing upwards. The tip is split. Gonopodial rays 5a and 5p are unserrated and do not reach the tip. Gonopodial ray 5p has a retrorse spine, which is more weakly developed at the end of ray 5a.

Description of the types.—The holotype is a male, 20.6 mm SL. The body has seven vertical stripes that extend from the middle of the body to the middle of the caudal peduncle. This is combined with a reticulate pigmentation pattern that is dorsally darker than ventrally. The dorsal fin reaches halfway from the base of its last ray to the base of the caudal fin. The caudal fin is clear, whereas the dorsal fin has a median basal blotch and has a dark margin. The female allotype is 23.1 mm SL. Pigmentation and scale counts are like those noted on the holotype. It has six dorsal fin rays and eight anal fin rays. The caudal fin rays are broken.

The meristic data are like those recorded for *P. caucana.* There are 25 scales in a lateral series, no more than 14 scales around the caudal peduncle and 16 scales around the body. Unfortunately, the caudal fins and the dorsal fins are damaged. *Poecilia wan-*

Fig. 3. *Poecilia wandae,* (a) holotype, (b) allotype.

dae resembles *P. caucana* in gonopodial characters. Gonopodial ray 3 has the first two segments unserrated; all other segments are serrated on both sides. The fleshy palp covers the tip. Gonopodial ray 4a has unserrated segments, with the last segment bending down. Gonopodial ray 4p has seven unserrated distal segments, the last segment bends upwards, splitting the tip. Gonopodial rays 5a and 5p are unserrated, both

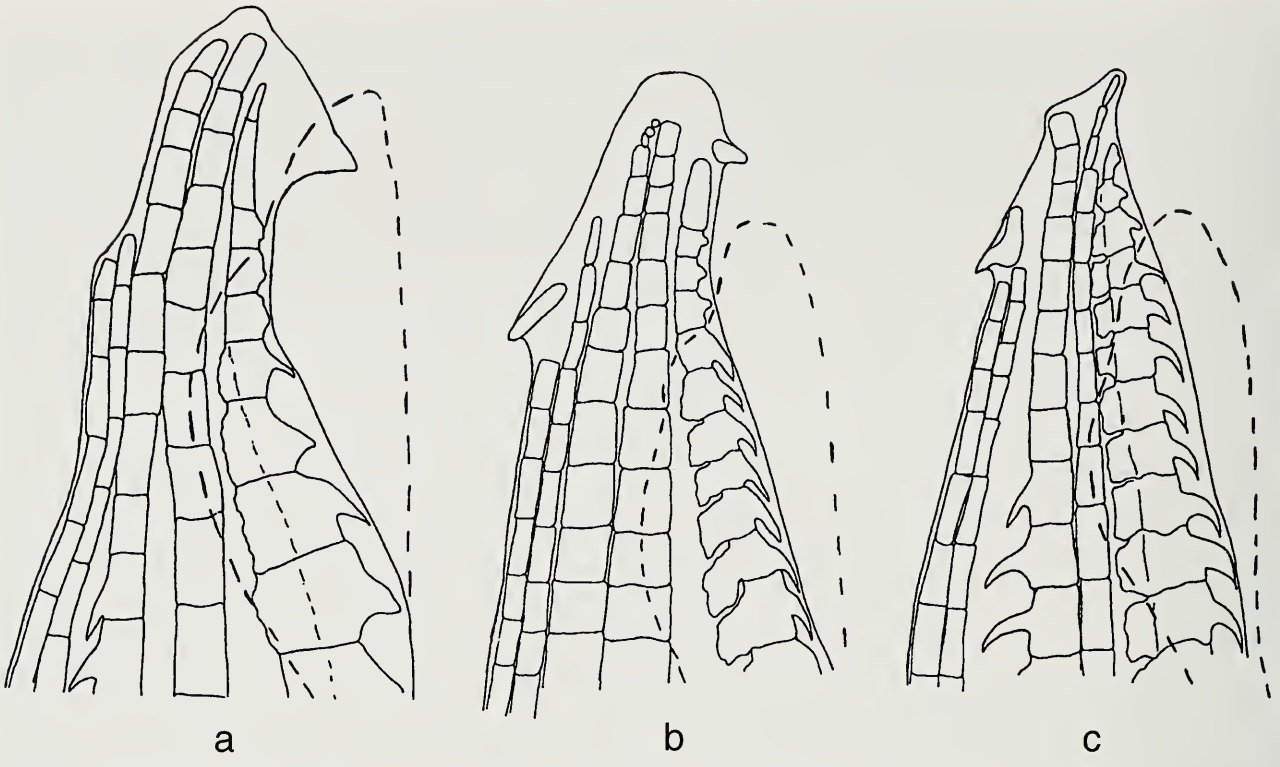

Fig. 4. Tips of gonopodia of (a) *Poecilia koperi,* (b) *Poecilia boesemani,* (c) *Poecilia wandae.*

do not reach the tip. Gonopodial ray 5p has a spinous retrorse extremity. Proportional body measurements in Table 2.

Distribution.—This species is known from several river systems west of the Maracaibo basin.

Etymology.—This species is named after Vanda Marisa Freitas de Leite, who wishes to be called Wanda.

Remarks.—Some specimens collected from the population of the Rio San Juan/ Rio Negro drainage are pale, without any specific marking with the exception of two specimens. One female has a distinct black spot on the caudal base and another spot on the left side of the body under the dorsal fin. Another female had a similar spot on the left side at the upper margin of the caudal base. The number of specimens available, however, was too limited to decide whether these latter populations are either specifically distinct, or only color morphs of *P. wandae.*

Discussion

The South American species of *Poecilia* inhabit mostly peripheral habitats, i.e., coastal areas or islands. *Poecilia sphenops* and *P. vandepolli* do not occur on the Venezuelan mainland (Poeser 1992; present study), despite earlier reports (Schultz 1949, Feltkamp and Kristensen 1969). In the present paper, seven species from the northeastern part of South America are recorded. One of these species, *P. gillii* (Kner and Steindachner, 1864), also occurs in Central America, and one species, *P. vivipara,* extends from the Orinoco drainage and the Lesser Antilles south to Argentina. The re-examination of *P. vandepolli* confirmed past observations concerning character variation in this species, whereas examination of the Colombian and Venezuelan populations of mollies confirmed earlier conclusions (Poeser 1992) that the Venezuelan population are neither *P. sphenops* nor *P. vandepolli.* One of the new species described herein, *P. wandae,* is related to *P. caucana* based on its morphological and gonopodial characteristics.

Venezuela is divisible into four distinct biogeographical regions, viz., the Maracaibo basin, mainland Venezuela, the drainage of the Rio Orinoco, and the adjacent islands

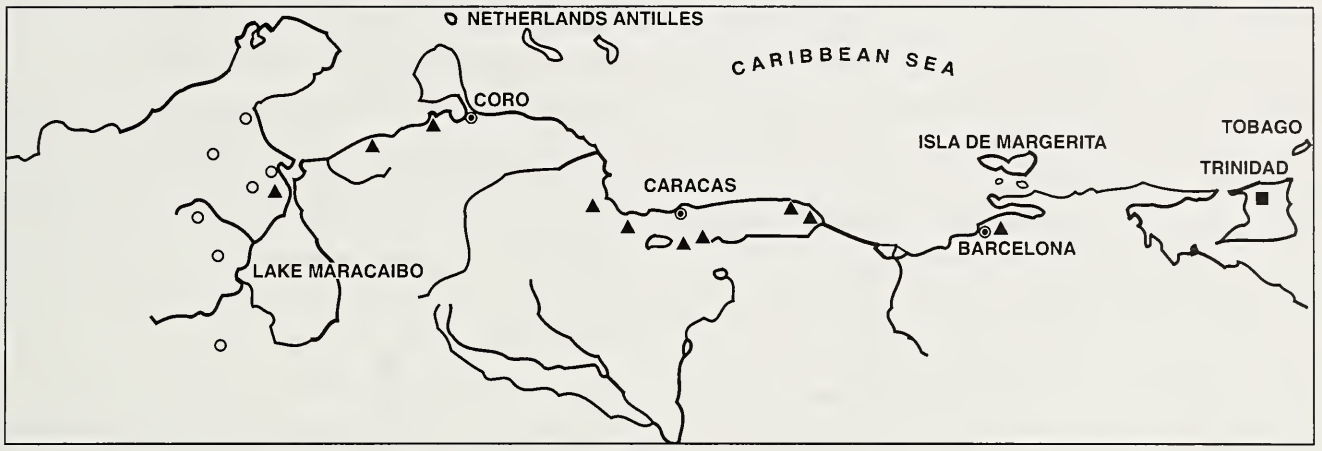

Fig. 5. Map of Venezuela. The locations of UMMZ material (=*P. koperi*) are noted with black triangles, the USNM material (=*P. wandae*) are open circles, the RMNH material (=*P. boesemani*) is a black square.

of the Lesser Antilles. Only one of the examined species occurs in more than one district, viz., *P. caucana* (along the Atlantic coast from Panama to the delta of the Rio Orinoco). In the Rio Orinoco, *P. vivipara* finds its northernmost mainland extension. *Poecilia vandepolli* and *P. boesemani* are endemic species located on islands adjacent to Venezuela. Comparisons with Central American mollies reveals that the species of *Poecilia* manifest a clinal reduction in body size and a decrease in meristic characters from north to south. *Poecilia mexicana,* naturally occurring on the Atlantic side of Mexico, has unicuspid inner teeth, nine dorsal fin rays, nine anal fin rays, 18 scales around the caudal peduncle, and two spines at the tip of the gonopodium (Table 3). Miller (1983) could not distinguish *P. mexicana* from *P. gillii,* and genetic data of *P. mexicana* from Vera Cruz and from Costa Rican populations (labeled "*P. gillii*") are virtually identical (Brett & Turner 1983, p. 136: cluster map of NEI identity values).

Why then separate *P. mexicana* from *P. gillii*? Villa (1982) and Bussing (1987) both mentioned two species fitting the descriptions given in the present paper. Although 29 scales in a lateral series are not typical for *P. mexicana* (cf. Menzel and Darnell 1973), Bussing (1987) nevertheless considered populations with this character as *P. mexicana.* The alternative hypothesis would be that *P. gillii* is a subspecies of *P. mexicana* with 16 scales around the caudal peduncle. The populations with 29 scales in a lateral series (Villa 1982; Bussing 1987) should then be considered another (possibly new) species.

Poecilia gillii has been reported to exceed 100 mm SL (Bussing 1987). The body size of the investigated specimens was always much less than 100 mm SL. In contrast to its variable body shape (Meek 1914, Meek and Hildebrand 1916), the meristic data are fairly constant. From El Salvador (Poeser 1995), through Nicaragua (Villa 1982) and Costa Rica (Bussing 1987) to Panama and Colombia (present study), *P. gillii* constantly displays nine anal fin rays, nine or ten dorsal fin rays, 16 scales around the caudal peduncle, and on average 27 scales in a lateral series. The only significant change in diagnostic characteristics is a reduction of the spine found on gonopodial ray 5p. The observed differences in gonopodial structures I regard as subspecific variation within *P. gillii.*

The next species in the Central to South American cline is *P. koperi,* found in Venezuela. *Poecilia koperi* differs from *P. gillii* in the number of dorsal and anal fin rays (8 versus 9 in *P. gillii*). The reduction of the gonopodial spine on ray 5p is complete in *P. koperi.* The next species south, *P. vivipara,* continues the trend of reduction, exhibiting 7 dorsal fin rays and a lack of all gonopodial extremities. In addition, *P. vi-*

Table 3.—Clinal variation in meristic data and gonopodial characters in 5 examined taxa, from north to south.

Species	Range	A	D	CPS	Gonopodial tip
P. mexicana	Atlantic coast from Texas to Costa Rica	9	9 or 10	18	spine on ray 3, spine on ray 5
P. gillii gillii	Pacific coast from Guatemala to Panama	9	9 or 10	16	spine on ray 3, spine on ray 5
P. g. cuneata	Panama and the Atlantic coast of Colombia	9	9 or 10	16	spine on ray 3
P. koperi	Colombia and Venezuela	8	8	16	spine on ray 3
P. vivipara	Venezuela to Argentina	8	7	16	no gonopodial spines

vipara has a median positioned humeral blotch and serrae on gonopodial ray 4a, unique characters in the subgenus, but not in the genus. In the subgenus *Lebistes* sensu Rosen and Bailey (1963), *P. reticulata* also has serrae on gonopodial ray 4a, *P. bifurca* exhibits the lateral body spot, and *P. picta* exhibits both the serrae on ray 4a and the lateral body spot.

An exception to these clinal variations is seen in *P. boesemani,* which occurs on Trinidad. *Poecilia boesemani* has a reduced body size, less anal fin rays and a reduced number of scales around the caudal peduncle than seen in *P. mexicana,* whereas the number of dorsal fin rays and the gonopodial characters are similar in these two species. Based on the last two similarities, Price (1955:7, 18) and Boeseman (1960: 122) presumed that *P. boesemani* was merely an introduced aquarium strain with the vernacular name 'Liberty molly'. *Poecilia boesemani* resembles western populations of *P. sphenops* in fin pigmentation and general morphology (Schultz and Miller 1971). The inner jaw dentition, however, is unicuspid versus tricuspid in *P. sphenops. Poecilia boesemani* differs from most Central American species in the number of anal fin rays (8 versus 9 in the other species), in the number of scales around the caudal peduncle (mostly 18 in the other species) and in female pigmentation (rows of black spots in *P. sphenops* and in *P. mexicana*). *Poecilia boesemani* more closely resembles *P. butleri,* another widely distributed Mexican species, in the number of anal fin rays; it differs, however, in dorsal fin pigmentation (distinct basal blotch in *P. butleri* [cf. Schultz and Miller, 1971]). Furthermore, *P. boesemani* and *P. butleri* are geographically the most separated species. *Poecilia boesemani* differs from *P. koperi* and *P. vandepolli* in the presence of distal spines on both gonopodial rays 3 and 5. Boeseman's (1960, p. 122) observation that "it lacks a distal retrorse segment on gonopodial ray 5", is erroneous (Fig. 4b). *Poecilia vandepolli,* occurring on the Dutch Lesser Antil-

les, also has a reduced body size, less dorsal fin rays, 16 scales around the caudal peduncle, and gonopodial characteristics like those seen in *P. vivipara.* It also has a humeral blotch, although it is found more anteriorly on the body than in *P. vivipara.*

The clinal variation is evident in *P. caucana* and *P. wandae. Poecilia wandae* is superficially like *P. caucana,* resembling it in size, scale counts, pigmentation, and gonopodial structures. It differs, however, in the number of anal fin rays (6–8 versus always 8 in *P. caucana*), dorsal fin rays (5–7 versus 7 or 8 in *P. caucana*), and in the absence of a membranous hook on gonopodial ray 3. The gonopodia of both species agree in several internal structures (Rosen & Bailey 1963:62, fig. 25B). Rosen & Bailey (1963) reported that this 'undescribed species', viz., *P. wandae,* was osteologically like *P. caucana,* as well as the Hispaniolan species of *Poecilia,* viz., *P. elegans, P. dominicensis* and *P. hispaniolana,* and "the smaller species of the *P. sphenops* group". Unfortunately, they did not specify to which species in the *P. sphenops* group they were referring. The occurrence of such similarities in widely separated species suggests that the osteological evidence could represent a primitive state. Furthermore, based on its gonopodial structures, it was suggested that *P. caucana* is related to the species of *Limia* of Hispaniola, and to the Central South American species of *Pamphorichthys* (Rosen 1975, Rauchenberger 1989). This would than place the origin of *P. caucana* and *P. wandae* from an ancestral species in South America at 80 to 70 Mya. (Pitman et al. 1990: fig. 2.5C). During this period, Hispaniola was situated between North and South America, as part of the great Arc of Proto-Greater Antilles. The morphological differences, i.e., the diversion from the "molly-geocline", as well as the osteological and gonopodial characteristics linking *P. caucana* and *P. wandae* with Hispaniolan and South Brazilian species, suggest a separate origin for these two species. The overall similarities in gonopodial structures, however, warrant their present inclusion in *Poecilia.*

Under a dispersalist scenario, one may conclude that members of the genus *Poecilia* entered South America after the completion of the Andean uplift and the formation of the Panamanian landbridge, i.e., about 4 Mya. (Pitman et al. 1990: fig. 2.5 F). This rapid dispersal and speciation resulted in subsequent differentiation from the Central American species of *Poecilia.* This hypothesis is confirmed by a molecular phylogeny presented by Breden et al. (1999), who concluded that *P. vivipara* was significally different from the species of the *P. sphenops* complex in Central America. Breden et al. (1999) suggested a separate taxonomic status for the *P. sphenops* complex and allocate these species, together with the broad finned mollies (cf. Miller 1983), in the subgenus *Mollienesia* (sensu Miller 1975). Rodriguez (1997) proposed a similar taxonomy based on a phylogenetic analysis of morphological characters. However, all three studies (Miller 1975, Rodriguez 1997, Breden et al. 1999) did not investigate the clinal variation in characters found in the present study. The suggestion of a separate taxonomic status for *P. vivipara* will be the subject of further investigations.

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Appendix 1.—Key to the species of the subgenus *Poecilia* (sensu Rosen and Bailey, 1963), south of Mexico.

1a. Inner jaw dentition tricuspid	*P. marcellinoi*
1b. Inner jaw dentition unicuspid	2
2a. Number of scales around the caudal peduncle 18	*P. mexicana*
2b. Number of scales around the caudal peduncle less than 18	3
3a. Number of scales around the caudal peduncle 16	4
3b. Number of scales around the caudal peduncle 14	100
4a. Number of anal fin rays 9	5
4b. Number of anal fin rays 8	7
5a. Body never with humeral blotch, never with 8 anal fin rays	6
5b. Body often with humeral blotch, sometimes with 8 anal fin rays	*P. vandepolli*
6a. Gonopodial tip with spiny hooks on ray 3 and ray 5p	*P. gillii gillii*[a]
6b. Gonopodial tip with spiny hook only on ray 3	*P. gillii cuneata*
7a. Gonopodial tip with spiny hooks on ray 3 and ray 5p	*P. boesemani*[b]
7b. Gonopodial tip without hooks or spines	8
8a. Gonopodial ray 4a never with dorsal serrae	*P. koperi*
8b. Gonopodial ray 4a with dorsal serrae	*P. vivipara*
9a. Number of anal fin rays 8	*P. caucana*
9b. Number of anal fin rays less than 8	*P. wandae*

[a] Specimens with a red dorsal fin are diagnosed *P. g. salvatoris,* unicuspid specimens with a caudal blotch are *P. g. caudata.*

[b] Miller (1983) reported *P. butleri* from El Salvador, fitting this description. However, he omitted the diagnostic characteristics for these populations.